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Tenedos: an early conquest of America (Araneae, Zodariidae)

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Tenedos: **an early conquest of America (Araneae, Zodariidae).** - Eight species of the genus *Tenedos* O.P.-Cambridge were known before its revision was started. Nearly 50 species are recognized so far.
A cladogram was established almost exclusively on the base of palpal characters since the somatic features are particularly stable. The scenario of the dispersion of *Tenedos*, based on the cladogram is as follows: as the ancestral species are widely scattered, it is likely that most of the South American continent or at least the semi-arid, non-forested parts, were already invaded before the split-up of Gondwanaland. With the development of the broad-leaved forest on the Cretaceous-Tertiary boundary, the distribution of this presumably initially xerophilous taxon, is likely to have shrunk considerably. However, a substantial number of species has apparently adapted to these novel circumstances. Later on, they colonized the Andes from north to south. This clade apparently also recolonized the Amazon-basin from the west. After the connection with North America through the Central American land bridge (about 3 myBP), three different radiations invaded Mexico. The northernmost region they reached is on the Chihuahuan-Coahuilan plateaus, about 300 km south of the Rio Grande. The success of *Tenedos* in Mexico, half of the species (20) so far known are from that country, might be explained by its apparent flexibility as it has representatives in a wide variety of habitats which had apparently not been colonized by spiders with a similar biology.

Key-words: *Tenedos* - Neotropical Region - phylogeny - radiation - distribution - male palp - historical biogeography.

INTRODUCTION

The zodariid fauna of South America is considered to be less rich than that of Africa and Australia. The reason for this assumption is that the two neotropical genera that have been revised so far, *Ishania* Chamberlin (Jocqué & Ubick 1991) and *Leprolochus* Simon (Jocqué 1988; Jocqué & Platnick 1989) are known so far only

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from a few species respectively 2 and 4. The African and Australian genera that have been revised tend to be much more speciose: *Diores* Simon for instance, contains 55 species (JOCQUÉ 1990; JOCQUÉ & DIPPENAAR-SCHOEMAN 1992), *Storena* Simon has 29 (JOCQUÉ & BAEHR 1992, 1995) and the number of *Asteron* species will exceed a hundred (BAEHR & JOCQUÉ 1996). The genus *Tenedos*, a purely New World zodariid genus, contains so far 8 species but a revision in preparation will raise the number to near 50. This is likely to be an underestimation as vast areas within the distribution range of *Tenedos* are still unexplored.

The present paper analyses the distribution of that genus and tries to reconstruct the history of its dispersion.

MATERIAL AND METHODS

The genus *Tenedos* has a remarkably stable somatic morphology whereas the palpal morphology is extremely variable. Since females are rare in collections the cladistic analysis is almost entirely based on male palpal morphology except characters 14 and 15 (table 1). The number of species considered was therefore limited to 35, as the remainder are only known from females so far. As an outgroup we used the genus *Platnickia* Jocqué, the sister-group of the large clade in which *Tenedos* takes a position near the base (JOCQUÉ 1991). The analysis was done with the program PeeWee (GOLOBOFF 1994). All characters were run unordered. The taxa were entered alphabetically except the first one which is considered the most plesiomorphic of the set. The combination of Whennig and Empezar with default concavity (K = 3) resulted in a single tree with weight 284.7, consistency index 0.46 and retention index 0.66. The tree was further analyzed with Macclade version 3 (MADDISON & MADDISON 1992).

TABLE 1

Character states in different species of *Tenedos*
(0 = plesiomorph; 1 - 8: apomorphic states)

1 **0 no patellar apophysis**
1 with dorsal apophysis in front;
2 " " " further backwards .

2 **0 retrolateral tibial apohysis (RA) on tibia with outgrowth** on dorsal margin small **and unmodified;**
1 RA: outgrowth elongate and with modifications;
2 RA: situated near ventral margin;
3 RA: broad and complex;
4 RA: appears double due to deep groove;
5 RA: bifid;
6 RA: very small;
7 RA: shifted towards dorsal side;
8 RA: absent.

3 **0 dorsal tibial apophysis (DA) absent;**
1 DA: tiny, separated by groove from RA;
2 DA: small, groove less obvious;
3 DA: outgrowth of posterior margin, poorly sclerotized
(dorsal swelling);

4 DA: large, strongly sclerotized, directed forwards;
5 DA: displaced to a lateral position, short hook;
6 DA: displaced to a lateral position, large;
7 DA: large, modified.

4 **0 ventral tibial apophysis (VA) absent;**
1 VA: unmodified, blunt;
2 VA: with sharp tip;
3 VA: with expanded tip.

5 **0 ventral haired swelling absent;**
1 ventral haired swelling displaced to lateral side;
2 ventral haired swelling present.

6 **0 no prolateral tibial apophysis**
1 prolateral apophysis present.

7 **0 embolus short, slender**
1 embolus long, slender and flexible;
2 embolus rigid;
3 embolus rigid, with distal extension.

8 **0 embolus originates far in front of tegulum**
1 base of embolus directed retrolaterad;
2 base of embolus directed backwards.

9 **0 suprategulum simple**
1 suprategulum grooved, broad, directed retrolaterad;
2 suprategulum grooved, directed backwards;
3 suprategulum bifid, extended in opposite direction of embolus, 1/4 length of cymbium;
4 suprategulum bifid, extended in opposite direction of embolus, 1/2 length of cymbium;
5 suprategulum bifid, extended in opposite direction of embolus, 3/4 length of cymbium;
6 suprategulum concave, directed prolaterad.

10 **0 tegular apophysis (TA) well developed with median groove**
1 TA membraneous;
2 TA membraneous, with sclerotized tip;
3 TA spoonshaped with membraneous base;
4 TA hook-shaped;
5 TA slightly curved and unmodified;
6 TA bifid.

11 **0 tegulum without swelling near base of embolus**
1 tegulum with swelling near base of embolus;
2 tegulum with apophysis near base of embolus.

12 **0 cymbial flange unmodified**
1 cymbial flange extended backwards.

13 **0 number of apical cymbial spines high >4**
1 number of apical spines = 4;
2 number of apical spines = 3;
3 number of apical spines = 2;
4 number of apical spines = 1;
5 number of apical spines = 0.

14 **0 abdominal pattern with many small patches and chevrons**
1 abdominal pattern complex without chevrons;
2 abdominal pattern simple with chevrons;
3 abdominal pattern simple (less than 8 patches).

15 **0 patellae III & IV with many spines**
1 number of spines less than, or equal to 2 prolateral and 2 dorsal ones.

16 **0 palpal tibia without a strong dorsal spine**
1 palpal tibia with a strong dorsal spine.

RESULTS AND DISCUSSION

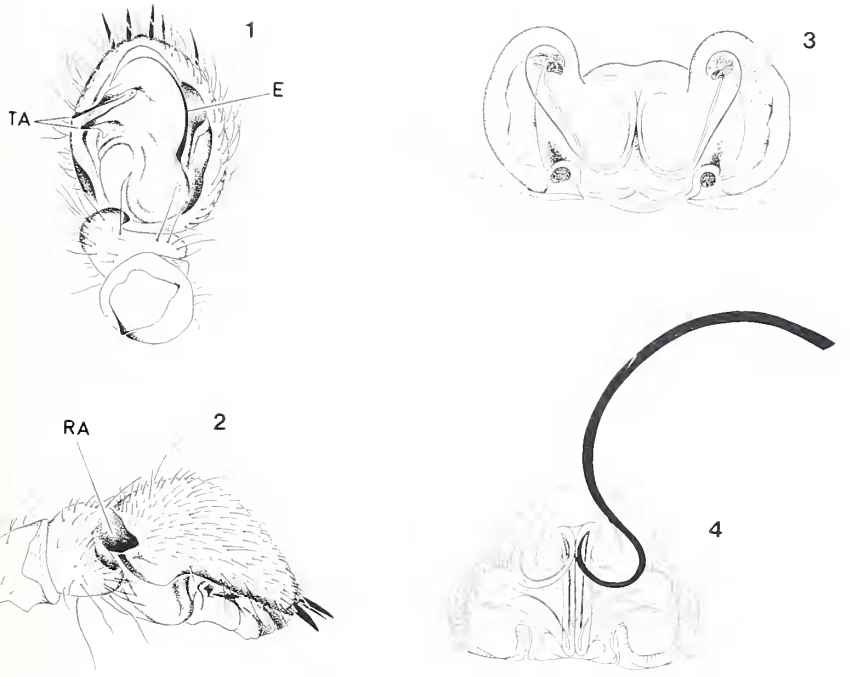
Analysis of the male palpal morphology resulted in 14 characters. 2 additional somatic characters (14 and 15) were added to this. 12 of these are multistate characters (table 1 and 2). A detailed explanation of these characters will be published in the revision of *Tenedos* (Jocqué & Baert, in preparation). It should be mentioned

TABLE 2.

Matrix of characters based on table 1.

species	clade symbol	character states
01	▲	0000000000 000000
02	▲	0200000011 000000
03	▲	0500001114 000200
05	▲	0001001114 113300
06	▲	0400100011 200110
07	▲	0623001124 002100
07	▲	0101000015 001010
08	▲	0100000000 002210
09	▲	0340001134 002310
10	●	0330001252 104210
11	●	0320002241 003210
12	●	0671001212 003310
13	●	0001001216 003310
14	●	0001001214 013310
15	●	0403001113 213110
16	●	0301000144 013310
17	●	0401011144 111110
18	●	0401011116 213210
19	●	0671011254 013310
20	●	0302010144 012310
21	●	0302010144 011310
22	★	0300002161 103310
23	★	0761001165 100210
24	★	0761002164 000310
25	★	0761002064 000310
26	▼	0320202142 103210
27	▼	0870202134 113111
28	▼	2660202164 103210
29	▼	1350203134 102110
30	▼	1760003134 103310
31	■	0430201152 103310
32	■	0330201152 005110
32	■	0670201154 003310
34	■	0310200252 003310
35	■	0330201252 003310

though that the plesiomorphic condition of the male palp of *Tenedos* is characterized by its simplicity (figs 1, 2). The tibia has a single dorsolateral apophysis which tends to shift to a more lateral position in more apomorphic species. The embolus is short and may be flexible or rigid but originates on the prolateral side of the tegulum. The

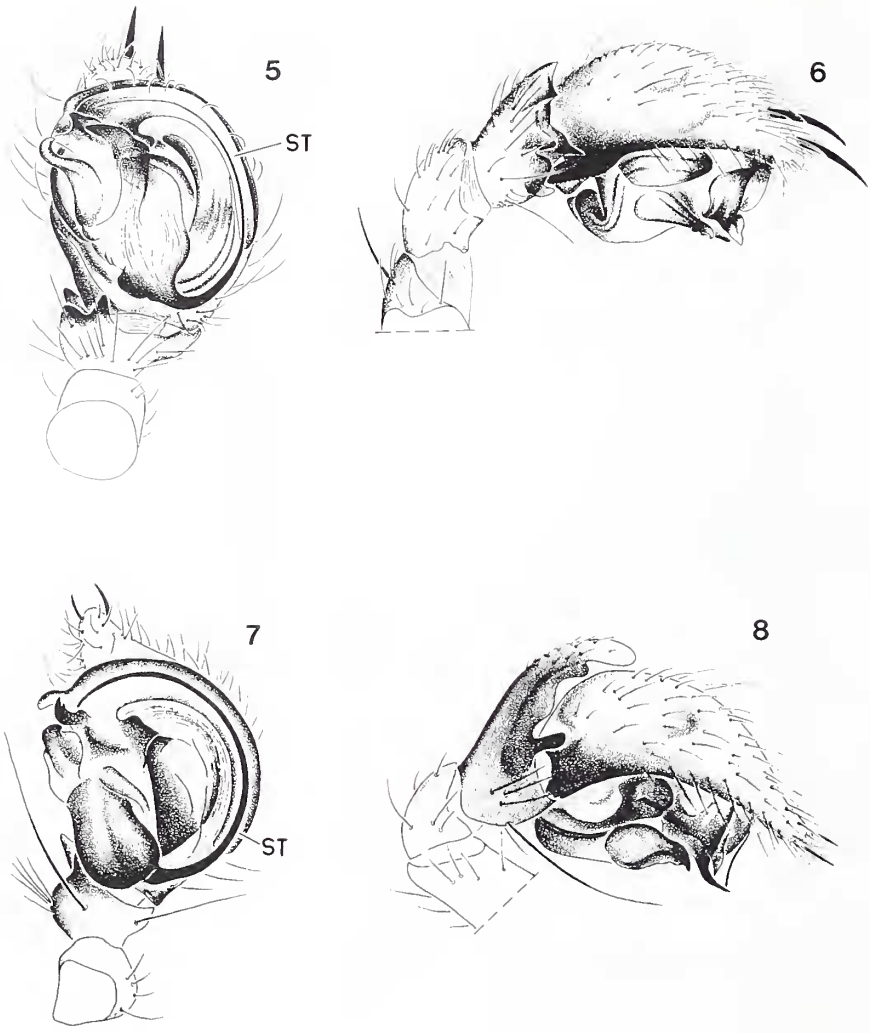


FIGS 1-4

Figs 1-2: Simple male palp (▲, n° 1) showing short embolus (E) originating on prolateral side of the tegulum, the simple tegular apophyses (TA), and the retrolateral tibial apophysis (RA) in a dorsolateral position. Figs 3-4: Simple epigyne (clade ▲, n° 6) (fig. 3) with short entrance ductsand complex epigyne (clade ■, n° 31) (fig. 4) with stuck embolus.

tegulum has two simple tapering apophyses with converging tips. This character is the autapomorphy of the genus. Linked with this simple palp is an equally simple epigyne (fig. 3), characterized by short entrance ducts with a single bent leading to rather complex spermathecae. This poorly understood spermatheca is typical for many genera in the Zodariidae.

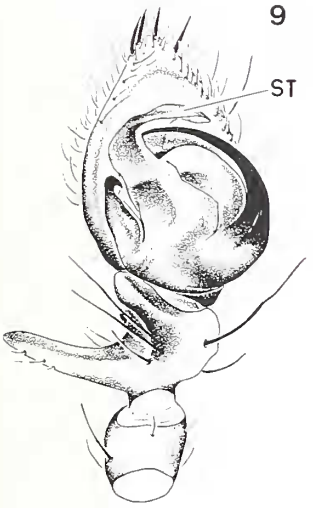
The evolution of the genus is characterized by an increasing complexity of the epigynes in which the number of bents is multiplied (fig. 4). The male palp goes through an evident parallel increase in complexity (figs 5-12). The most conspicuous changes are the increase in the number of tibial apophyses, the lengthening of the embolus and the complication of the tegular apophyses. The evolution of the latter shows a certain parallelism with what happens in *Asteron* (JOCQUÉ & BAEHR 1996). In that genus the tegular apophysis becomes a functional conductor developed in the opposite direction of the embolus. In most other Zodariidae and in spiders in general, the conductor points in the same direction as the embolus. Whereas the ever increasing length of the embolus leads to a spectacular palp in *Asteron*, the evolution

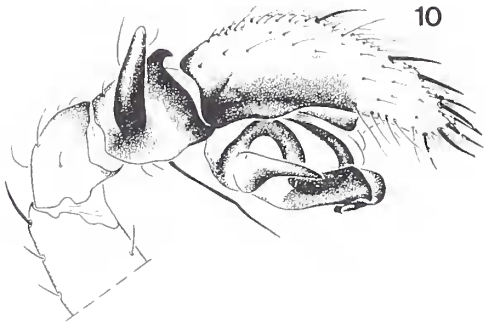


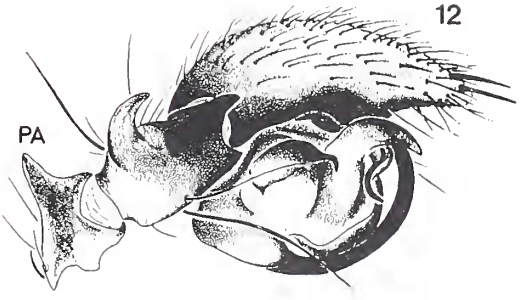
FIGS 5-8

Examples of palps of the clade (●, n° 19) (figs 5-6) and of the clade ■ (n° 33) (figs 7-8) showing complex palpal tibia and the backward extension of the suprategulum (ST).

takes another direction in several clades of *Tenedos*. Instead of further lengthening, the embolus becomes rigid and eventually develops a distal extension (figs. 9-12). This phenomenon is characterized by a parallel shortening of the conductor (suprategulum). The development of a dorsal patellar apophysis is the latest development in one of the most apomorphic clades (fig. 12).







FIGS 9-12

Examples of palps of the clade (★, n° 24) (figs 9-10) showing rigid embolus and reduced suprategulum (ST) and of the clade ▼ (n° 30) (figs 11-12) showing rigid embolus with extension (EE) and patellar apophysis (PA).

According to the cladogram (fig. 13) the present distribution of *Tenedos* (figs. 8, 9) can be explained as follows: the most plesiomorphic species (▲) are found around the Amazon Basin (fig. 14). This corroborates the idea that Zodariidae were initially spiders adapted to arid or semi-arid habitats, or at least habitats with a marked dry season. The majority of South America is supposed to have had a xerophilous vegetation at the time Gondwanaland split up (ENDRÖDY-YOUNGA 1995). Ancestors of the present-day *Tenedos* species are therefore supposed to have colonized a large part of the subcontinent until their habitat shrunk as a result of the expansion of the rainforest. Due to alternating forest expansion and contraction (see LOURENÇO 1986), the habitat of the ancestral *Tenedos* was fragmented. The subsequent isolation of the populations resulted in different species which have apparently been separated for a long time as can be deduced from the ladder-shape of the inferior part of the cladogram.

The large radiations in *Tenedos* apparently only began after the connection of North and South America. This happened about 3 mybp when the Caribbean plate filled the gap between the North American and the South American plates (MALFAIT & DINKELMAN 1972). Thanks to the low dispersion speed of zodariids and their usually small distribution areas, it is possible to follow the evolution of the clades in

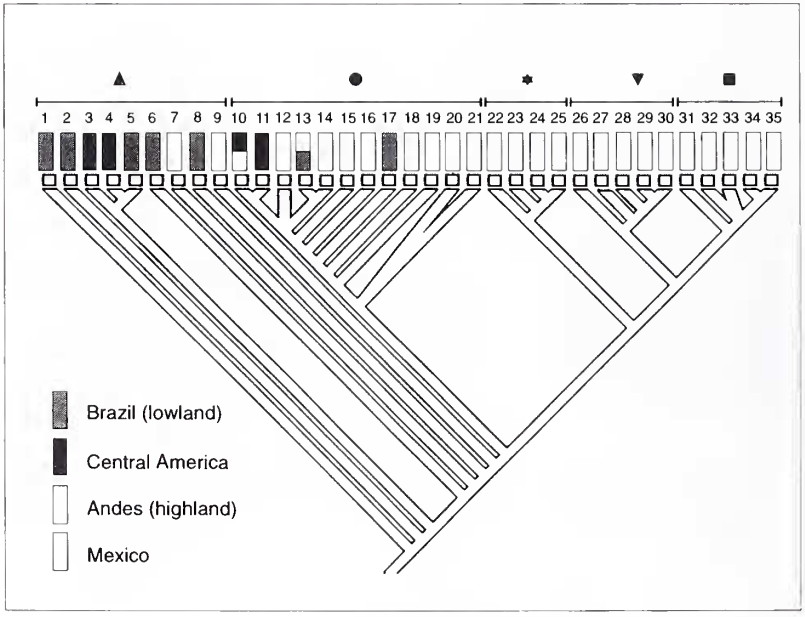


FIG. 13

Cladogram of species of *Tenedos* for which males are known showing symbols for the main clades and numbers of the species used in the distribution maps, showing general area from which the species is known.

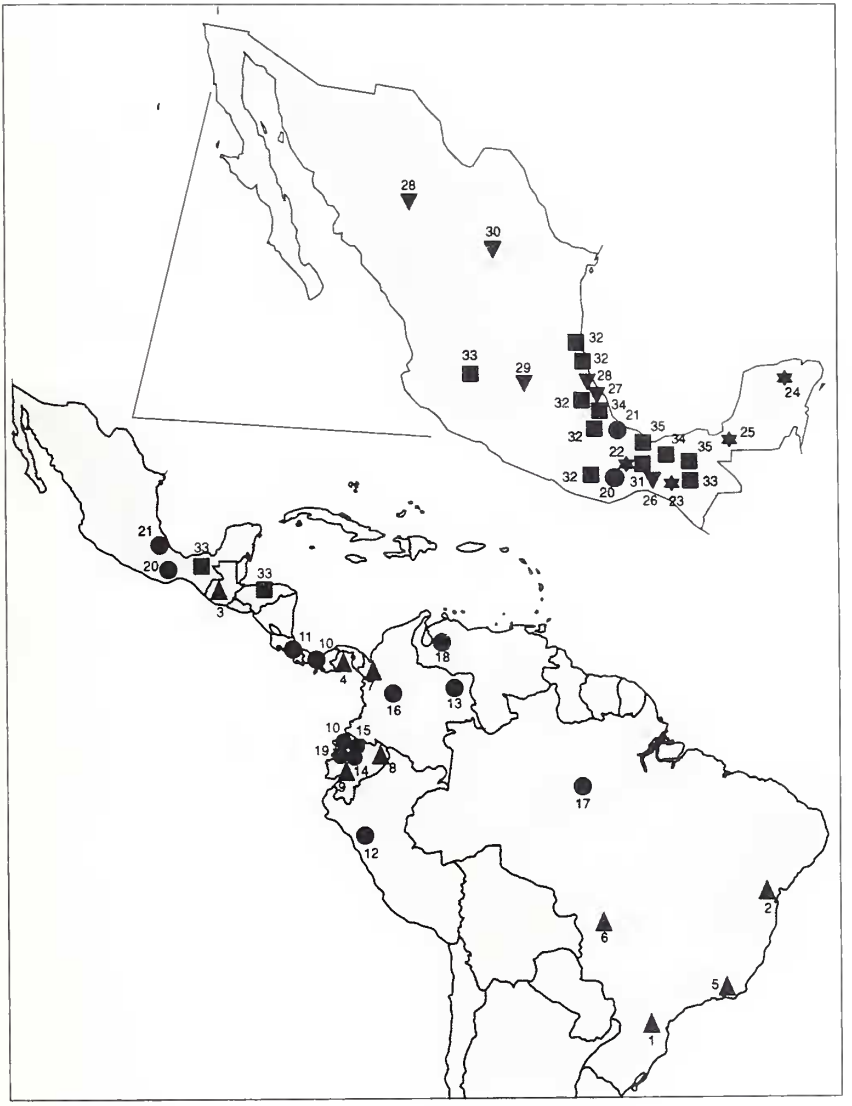


FIG. 14

Distribution map of species of *Tenedos* for which the male is known. Except for four species (n° 10, 32, 33 and 34) most species are only known from one locality which is an indication for their small distribution area.

FIG. 15

Reconstruction of the hypothesized dispersion history of *Tenedos* (for explanation see text).

space (fig. 15). According to the cladogram some of the more plesiomorphic species succeeded in reaching Central America. From there on a rapid radiation took place. Three clades (▼, ■ and ★) invaded North America (Mexico) from south to north whereas a fourth one (●) invaded South America along the Andes from north to south. The similarity with the historical conquest of South America in the 16th cen-

tury with main incursions into Mexico and along the Andes in South America, explains why we called the present distribution of *Tenedos* the result of an "early conquest" of the New World. This is also the reason why many of the species to be described will receive names of the tribes that were exterminated by the conquistadores.

The largest clade (●) also invaded the Amazon lowland and is supposed to be of recent origin (less than 3 my BP) just as the purely Mexican clades. The most plesiomorphic species in that clade are indeed also from Mexico.

It would seem that the plugging of the gap between North and South America triggered the radiations. For one reason or another the genus has become more plastic and was able to colonize different habitats ranging from dry desert (northern Mexico) to very wet rainforest (central Amazon basin). Mainly from the latter habitat many more species are expected as there are enormous gaps in our knowledge of that region.

CONCLUSION

The genus *Tenedos* is rich in species, most of which only evolved after the connection between North and South America, about 3myBP. The more plesiomorphic taxa in the genus, after having colonized most of the northern part of South America were apparently expelled from the wet central Amazon Basin. Starting from Central America, the main radiations travelled from south to north into Mexico and from north to south along the Andes into South America. The latter strain eventually also invaded the Amazon basin.

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